Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient

Meysick, Lukas

2019-08

Meysick , L , Ysebaert , T , Jansson , A , Montserrat , F , Valanko , S , Villnäs , A , Boström , C , Norkko , J & Norkko , A 2019 , ' Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient ' , Journal of Sea Research , vol. 150-151 , pp. 8-23 . https://doi.org/10.1016/j.seares.2019.05.001

http://hdl.handle.net/10138/332719
https://doi.org/10.1016/j.seares.2019.05.001

Full citation:
Meysick, L., Ysebaert, T., Jansson, A., Montserrat, F., Valanko, S., Villnäs, A., ... & Norkko, A. (2019). Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient. Journal of Sea Research, 150, 8-23.

Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient

Lukas Meysick [1*], Tom Ysebaert [2,3], Anna Jansson [4,5], Fransesc Montserrat [2,6], Sebastian Valanko [5,7], Anna Villnäs [5], Christoffer Boström [1], Joanna Norkko [5], Alf Norkko [5,8]

1. Environmental and Marine Biology, Faculty of Science and Engineering, Åbo Akademi University, Artillerigatan 6, 20520 Åbo, Finland (lukas.meysick@abo.fi, cbostrom@abo.fi)
2. Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research (NIOZ) and Utrecht University, 4400AC Yerseke, The Netherlands (Tom.Ysebaert@nioz.nl, montserrat@usp.br)
3. Wageningen Marine Research, Wageningen University and Research, Yerseke, The Netherlands (Tom.Ysebaert@nioz.nl)
4. Novia University of Apllied Sciences, 10600 Ekenäs, Finland (anna.jansson@novia.fi)
5. Tvärminne Zoological Station, University of Helsinki, J.A. Palméns väg 260, 10900 Hangö, Finland (anna.jansson@abo.fi, sebastian.valanko@ices.dk, anna.villnas@helsinki.fi, joanna.norkko@helsinki.fi, alf.norkko@helsinki.fi)
6. Department of Marine Ecology, Conservation and Management Institute for Oceanography - University of São Paulo, Praça do Oceanográfico 191, 05508-120 São Paulo (SP), Brazil (montserrat@usp.br)

7. International Council for the Exploration of the Sea (ICES), H. C. Andersens Boulevard 44-46, 1553 Copenhagen, Denmark (sebastian.valanko@ices.dk)

8. Baltic Sea Centre, Stockholm University, Stockholm, Sweden (alf.norkko@helsinki.fi)

Corresponding author:

*Lukas Meysick, Environmental and Marine Biology, Faculty of Science and Engineering Åbo Akademi University, Artillerigatan 6, FIN-20500 Åbo, Finland,

E-mail: lukas.meysick@abo.fi

Orcid ID: orcid.org/0000-0002-6217-4925

ABSTRACT

Foundation species host diverse associated communities by ameliorating environmental stress. The strength of this facilitative effect can be highly dependent on the underlying biotic and abiotic context. We investigated community level patterns of macrofauna associated with and adjacent to the marine foundation species eelgrass (*Zostera marina*) along a hydrodynamic stress gradient. We could demonstrate that the relative importance of this foundation species for its infaunal community increases with environmental variables associated with increasing hydrodynamic stress (depth, sand ripples formation, sediment grain size and organic content). Faunal assemblages in proximity to the *Zostera* patch edges, however, showed no (infauna) or negative (epifauna) response to hydrodynamic stress. Our study highlights that the facilitative outcome of a foundation species is conditional to the faunal assemblage in question and can be highly variable even between positions within the habitat.

Keywords: ecosystem engineer; *Zostera marina*; conditional facilitation; seagrass; habitat modification; foundation species

1. INTRODUCTION

It is increasingly recognized that facilitation by foundation species, and ecosystem engineers, has a profound influence on surrounding communities in both terrestrial and aquatic ecosystems (Dayton 1972, Jones et al. 1994, Bruno and Bertness 2001, Bruno et al. 2003, Ellison et al. 2005). Biogenic habitats such as salt marshes, seagrasses meadows, bivalve reefs and mangrove forests form vast seascapes and provide multiple important ecosystem services, including hosting diverse associated communities (Beck et al. 2001, Boström et al. 2011). By ameliorating e.g. physical exposure or nutrient availability, they promote the occurrence of other local species. Efforts that aim to resolve underpinning mechanisms of positive interactions continue to increase (Michalet and Pugnaire 2016). As such the Stress Gradient Hypothesis (SGH) predicts that facilitation will become more important in stressful than in benign environments (Bertness and Callaway 1994). A broadened understanding of facilitation provided by ecosystem engineers has great relevance for successful conservation and restoration efforts in biogenic habitats (Cordero et al. 2012, Sharma et al. 2016). Although the concept of facilitation is an inherent part of ecological theory and the supporting mechanisms are widely acknowledged, our knowledge of its conditionality remains fragmentary. This has led to discussions about the generality of the SGH (Maestre et al. 2005, Lortie and Callaway 2006, Maestre et al. 2009, Holmgren and Scheffer 2010, He et al. 2013), implying that the outcome of positive species interactions is highly dependent on environmental context and the interacting species in question (Norkko et al. 2006, Kawai and Tokeshi 2007, Bulleri et al. 2011, Jurgens and Gaylord 2016). Moreover, these discussions emphasize that facilitation theory and the underpinning functional relationships need to be studied across a wide range of abiotic and biotic gradients and ecosystems.

Plant-plant interactions in terrestrial environments have received broad attention (Brooker et al. 2008, Bulleri 2009). In comparison, aquatic environments, and most notably marine subtidal habitats, remain understudied in terms of facilitation (Bulleri 2009). The majority of

82 studies describing the conditionality of facilitation in subtidal habitats have either addressed
83 intraspecific interactions (Wernberg et al. 2010, Bennett and Wernberg 2014, Bennett et al.
84 2015) or mutualism between two species (Bulleri et al. 2011, Bennett et al. 2015), but the
85 potential facilitation effect of an engineering species on its broader associated community has
86 been widely ignored. Earlier works by Woodin (1981) and Gallagher et al. (1983), for
87 example, highlight the importance of benthic tube-builders for predator refuge and natural
88 succession. Norkko et al. (2006) and Lohrer et al. (2013), have further revealed how
89 environmental conditions can inhibit facilitation of a subtidal benthic ecosystem engineer and
90 result in a decline in associated community abundance and diversity when biotic or abiotic
91 stress increases. This suggests that our understanding of stress amelioration by an ecosystem
92 engineer and its conditionality are insufficient and further attention is needed.
93 Seagrasses are important ecosystem engineers that possess a pronounced engineering
94 capacity resulting in a strong influence on multiple abiotic and biotic processes and
95 subsequent ecosystem services (Heck and Orth 1980, Fonseca et al. 1982). Seagrasses are,
96 however, simultaneously subjected to a multitude of anthropogenic stressors (Boström et al.
97 2011) causing local and global declines (Waycott et al. 2009), potentially compromising their
98 future role in marine coastal ecosystems. In accordance with ecological theory, these habitats
99 should be particularly important in maintaining benthic communities and promoting
100 biodiversity in physically stressful environments. As seagrass meadows significantly modify
101 their environment through e.g. attenuation of waves, reduction of current flow and provision of
102 below- and above-ground complexity (Fonseca et al. 1982, Fonseca and Cahalan 1992,
103 González-Ortiz et al. 2016), they are assumed to extend the realized niche of associated
104 invertebrates towards more unfavourable conditions (Bruno et al. 2003).
105 Here we present a study novel to subtidal facilitation theory by studying species and
106 community level patterns along a physical stress gradient dominated by the foundation
107 species, eelgrass (*Zostera marina*). Specifically, we predicted that *Zostera* patches located

along a depth gradient perpendicular to the shoreline will experience more hydrodynamic stress in terms of wave exposure when depth and distance to the shoreline decrease. By comparing invertebrate community variables between the seagrass patch interior, the patch edges and the adjacent bare sediments along this gradient, we aimed to enhance our understanding regarding the conditional outcome of facilitation by an ecosystem engineer. The study system is conceptualized in Fig. 1 illustrating how faunal community variables potentially change with increasing physical exposure. We hypothesized, that:

1. With increasing exposure, environmental conditions will negatively affect the local community in unprotected bare sediments (Fig. 1a). Facilitation by *Zostera,* simultaneously, will increase in importance for the local benthic community when environmental stress increases (Fig. 1c).
2. Facilitation will be less pronounced and more variable at seagrass edges compared to the interior, as the edges represent abrupt transitions between vegetated and bare habitats, highly exposed to variable hydrodynamic conditions (Fig. 1b).
3. Sediment infauna and leaf epifauna will respond differently to the ecosystem engineering by *Zostera*.

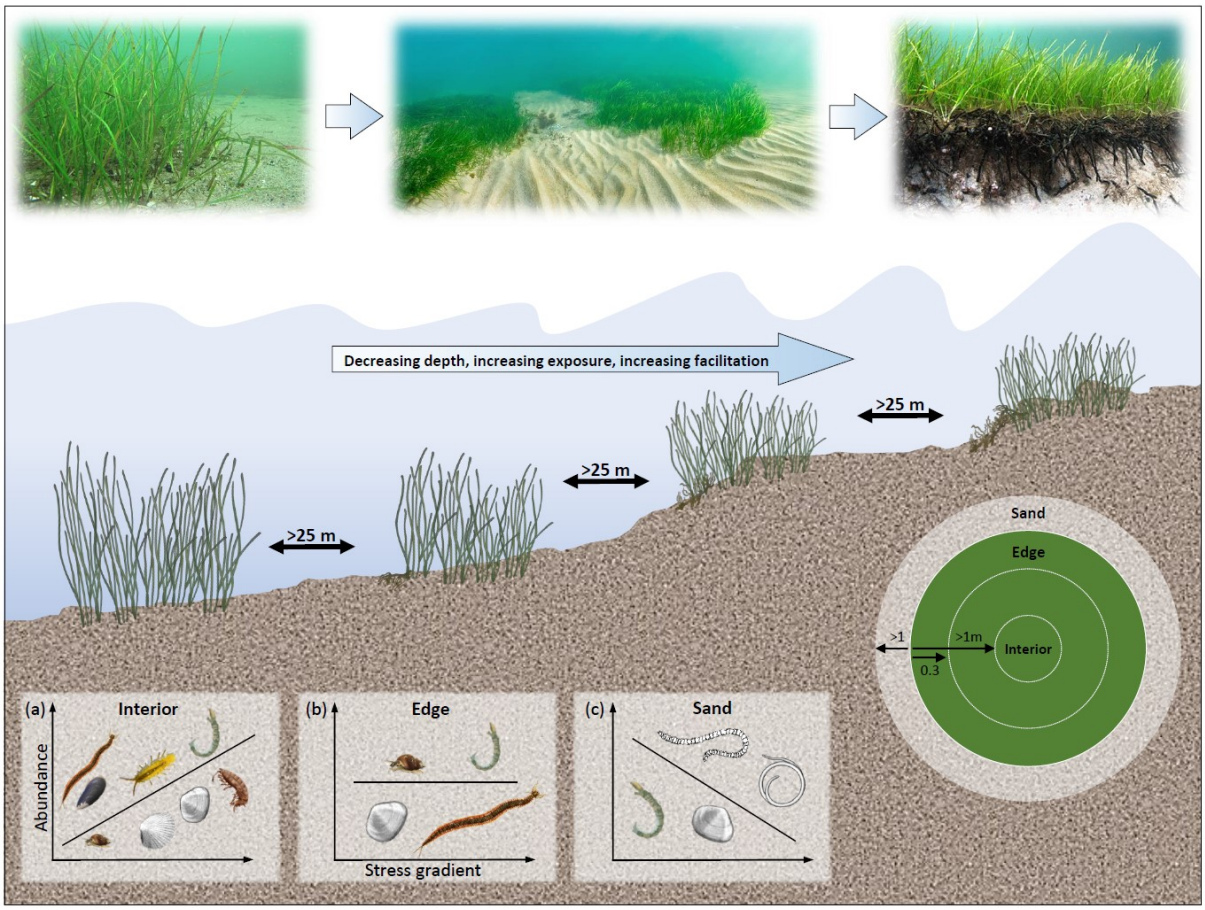


Figure 1: Conceptual model of the experimental setup illustrating how the benthic invertebrate community relative to seagrass patches (a: patch interior, b: patch edge, c: adjacent bare sand) and the edge structure of the seagrass patches (photos) are assumed to change along a gradient of decreasing depth and increasing physical exposure. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Photography supplied courtesy of Christoffer Boström (cbostrom@abo.fi, left) and Pekka Tuuri (pekka.tuuri@kolumbus.fi, mid and right).

2. MATERIAL AND METHODS

2.1. Study design and field sampling

Sampling was conducted in a shallow exposed sandy embayment at the Hanko peninsula, SW Finland (Fig. 2). In this region, *Zostera* meadows extend from the shoreline several hundred

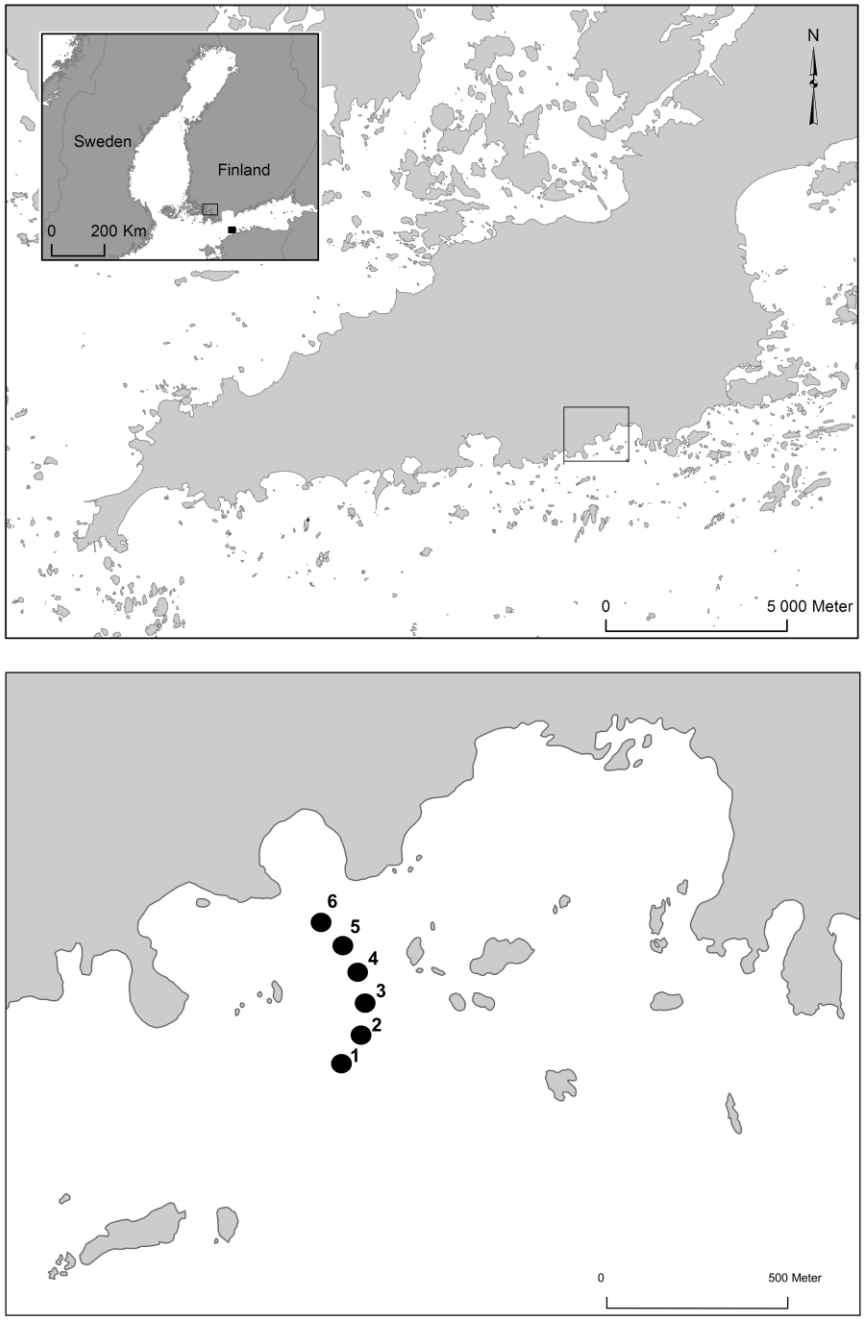


Figure 2. Study site with sampling locations (59°49’ N; 23°09’ E) at the Hanko peninsula, SW Finland, northern Baltic Sea.

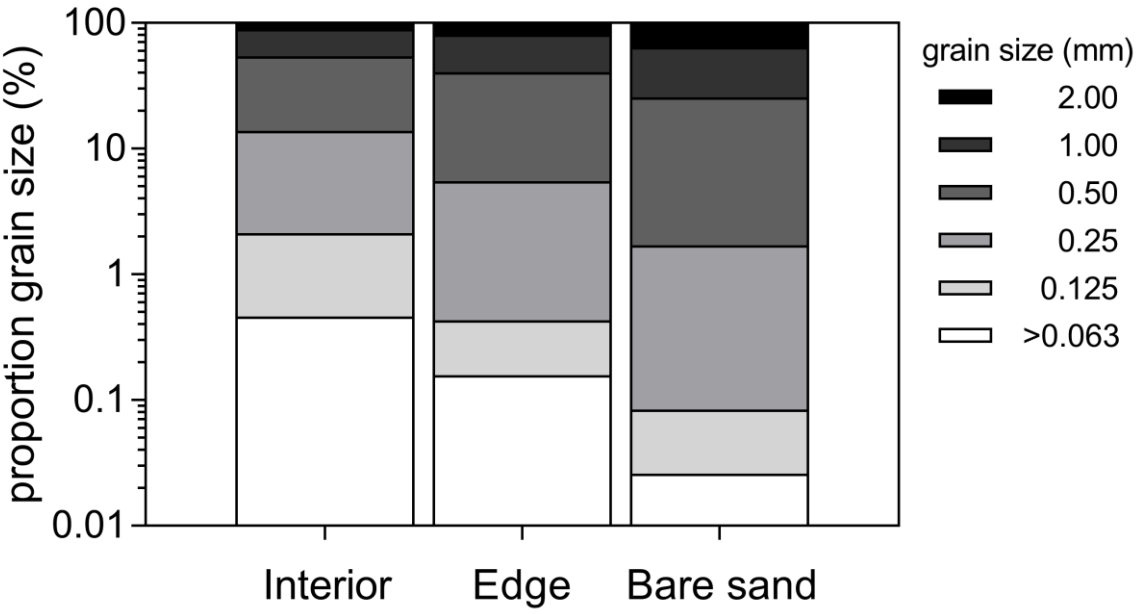
meters seawards (1-6 m depth range, Boström et al. 2014). Although there are some small islands in the vicinity, the area is exposed to the predominant southwesterly winds (Valanko et al. 2010). The seagrass in the embayment was comprised of a mosaic of habitat patches within unvegetated sandy sediments. Six separate *Zostera* patches (hereafter P1 - P6, with P1 being located most distant to and P6 closest to the shore) at an interval of min. 25 m were chosen for sampling. The selection criteria for the patches were: 1) to have a diameter of at

146 least 10 m, 2) to show a distinct seagrass/sand boundary and 3) to be aligned along a depth
147 gradient perpendicular to the shoreline, which served as a proxy for exposure. For each
148 *Zostera* patch three habitats for sampling were defined, which were all located towards the
149 seaward side of each patch: the patch interior >1 m inside from the seagrass/sand boundary
150 (I), the patch edge 0.3 m inside from the seagrass/sand boundary (E), and the adjacent bare
151 sand habitat (B) 1-3 m outside from the seagrass meadow (Fig. 1).
152 Samples of biotic and abiotic variables were collected by SCUBA diving within one
153 week from the end of August until the beginning of September 2008. For quantification of
154 sediment parameters, five replicate samples of the top 2 cm of the sediment were obtained
155 from each *Zostera* patch in all three habitats using syringes of 2.1 cm diameter. To quantify
156 *Zostera* plant characteristics, three replicate samples were collected at each patch from the
157 edge and interior of the meadow. Below-ground roots and rhizomes were collected by
158 pushing a core (Ø 13.5 cm) into the sediment and collecting all material into a bag. Above-
159 ground plant material was taken with an Ø 29 cm core. The same samples were used to collect
160 mobile leaf epifauna from the *Zostera* interior and edge at each patch. For quantification of
161 benthic infauna, five replicate samples from each habitat (interior, edge, bare sand) at each
162 patch were taken by pushing a core (Ø 5.6 cm) 10 cm into the sediment.
163 For further quantification of potential wave energy, ten randomly chosen sand ripples
164 were measured in length and height in the bare sand habitat of each patch. The ripple index,
165 i.e. the resulting quotient of length and height relates to the orbital diameter of surface waves
166 at seafloor level ([34]Clifton and Dingler 1984).
167 *2.2.Laboratory analysis*
168 The grain size distribution of the sediment samples was analyzed by dry sieving methods. The
169 finest fraction (< 1 mm) was further analyzed with a Malvern laser diffraction instrument.
170 Grain sizes were classified into size class fractions according to the Wentworth scale

171 (Wentworth 1922). Organic content of the sediment was measured as loss on ignition (LOI) in
172 6 h at 440°C, after drying the samples at 60°C for 48 h.
173 Root and rhizome samples were rinsed and *Zostera* below-ground and above-ground
174 biomass was determined by weighing after drying to constant weight at 60 °C. Shoots in each
175 sample were counted and average shoot length was calculated based on 10 randomly chosen
176 shoots. Samples of in- and epifauna were sieved over a 0.5 mm sieve, preserved in 70 %
177 ethanol and stained with rose bengal. Macrofauna was subsequently counted and identified to
178 the lowest practical taxonomic level.
179 *2.3.Statistical analyses*
180 Local biotic and abiotic conditions per patch and habitat were assessed by means of plant
181 variables (i.e., shoot density, above-ground biomass, below-ground biomass, shoot length),
182 contribution of grain size classes and sediment LOI. Differences were analyzed using a two-
183 way analysis of variance (ANOVA), with Habitat and Patch as fixed factors. When Habitat ×
184 Patch interactions were found, pairwise differences were assessed using Tukey's HSD *post-*
185 *hoc* multiple comparisons test. To contrast potential differences in facilitative effects between
186 the habitats, mean infaunal and epifaunal abundance and diversity (taxa richness) were
187 subsequently analyzed using Students t-test (contrasting patch edge and patch interior
188 epifauna) and one-way ANOVA (contrasting bare sand, patch edge and patch interior
189 infauna). To meet assumptions for parametric testing, homoscedasticity was tested with the
190 Brown-Forsythe Test and normality of residuals using a Shapiro-Wilk Test. Additionally,
191 histograms, Q-Q plots and variance plots were visually assessed to support assumptions for
192 the use of parametric tests. When necessary, data was appropriately transformed using a
193 square root or natural log+0.5 transformation (see Appendix Table A1). In the case the
194 assumptions for parametric testing were not met, non-parametric equivalent tests (Mann-
195 Whitney *U* test, Kruskal-Wallis Test) were used, followed by Dunn's Test as a corresponding

196 *post-hoc* multiple comparison. All univariate analyses were done using R (R Development
197 Core Team, 2017).
198 The hydrodynamic regime can have strong effects on local sediment properties. Particles
199 of 0.18 mm diameter are expected to be transported first by currents and waves, and thus the
200 proportion of fine sand (0.125-0.2mm, see Wentworth 1922) can give some indication of
201 underlying hydrodynamics (Gray and Elliott 2009). With increasing exposure, sediment
202 organic content typically decreases (Elliott et al. 1998, Samper-Villarreal et al. 2016), while
203 median particle diameter (d_{50}) typically increases (Elliott et al. 1998).
204 To characterize prevailing physical exposure due to wave and current forces along the six
205 habitat patches, we conducted a principal component analysis (PCA) that, additionally to
206 water depth and sand ripple index, took into account d_{50}, LOI and % fine sand outside of the
207 habitat patches. The PCA was performed on a correlation matrix of untransformed data to
208 account for scale differences between parameters. Resulting PC1 scores were used as an
209 adjusted exposure proxy for each habitat patch. This approach has the advantage of returning
210 relative multivariate distances. Thus an integrated relative exposure metric, i.e. an
211 environmental gradient, can be determined across the habitat patches (Ter Braak and Prentice
212 1988). This allows for regression-based techniques, combining potentially co-correlated
213 parameters on hydrodynamics into a latent variable in further analyses (see below).
214 We applied linear regression analysis to assess the functional relationship between the
215 resulting exposure proxy (as described by PC 1) and plant variables at the *Zostera* interior and
216 edge as well as between exposure and the associated fauna in the *Zostera* interior, the edge
217 and the bare sand separately. The ratio between interior and bare sand infauna abundance was
218 then used to assess a potential relative community effect of facilitation along this
219 environmental stress gradient. In order to explore the mechanisms responsible for facilitation,
220 linear regression of fauna with plant and sediment parameters was investigated. Furthermore,
221 dissimilarity percentages (SIMPER) were calculated between each location and patch using

222 Bray-Curtis measure of similarity on square root transformed abundance data to assess
223 changes in species composition and detect main beneficiaries, i.e. species that benefit from
224 *Zostera* along the gradient (PRIMER 6, Clarke and Gorley 2006).
225
226 3. RESULTS
227 *3.1.Environmental characteristics*
228 Analysis of grain size distribution and organic content revealed significant differences among
229 habitats and patches as well as Habitat × Patch interactions (Appendix Table A1). Grain sizes
230 below 0.5mm increased, while those larger than 0.5mm decreased in proportion towards the
231 patch interior (Fig. 3). Organic content increased towards the patch interior. In all three
232 habitats (patch interior, patch edge, bare sand) the lowest proportion of fines and highest
233 proportion of very coarse sand was found at patch P4.



234
235 **Figure 3.** Average grain size distribution at the *Zostera* interior, *Zostera* edge and
236 adjacent bare sediments examined across the whole exposure gradient (n=30 for each
237 habitat).

238 The highest proportion of fine and lowest proportion of very coarse sand were observed at the
239 innermost shallowest patch P6 and at the outermost deepest patch P1.
240 Similarly, median grain size (d_{50}, mm) in all three habitats was highest at P4 and lowest at P1.
241 Organic content (% LOI) peaked at P1, while lowest proportions of organics were found at
242 P5. Mean values for sediment properties can be found in the Appendix (Table A1).
243
244 *3.2.Seagrass characteristics*
245 Neither shoot density nor above-ground biomass (AB) showed significant differences
246 between edge and interior and among patches, though a Habitat × Patch interaction could be
247 detected (Appendix Table A1, Habitat × Patch interaction; shoot density: $p = 0.049$ and AB: p
248 $= 0.035$). Tukey multiple comparison between means, however, could not reveal pairwise
249 significant differences. Below-ground biomass (BB) was significantly higher in the *Zostera*
250 interior (Appendix Table A1; $p < 0.001$) but showed neither differences among the six
251 patches nor a Habitat × Patch interaction. Shoot length differed significantly between interior
252 and edge (Appendix Table A1, $p < 0.001$), and among patches ($p < 0.001$) and further showed
253 a Habitat × Patch interaction ($p < 0.001$). Mean values for plant variables at each patch and
254 habitat are summarized in Appendix Table A2.
255
256 *3.3.Invertebrate community*
257 Total infaunal abundance differed significantly between the three habitats with the highest
258 abundances in the *Zostera* interior, followed by the edge and lowest abundances in the bare
259 sand (Fig. 4a). Number of taxa was significantly higher in *Zostera* than in the bare sand, but
260 differences between *Zostera* interior and edge could not be detected (Fig. 4b).
261 In terms of species, the tube-building spionid *Pygospio elegans* had highest abundance in
262 the *Zostera* interior and lowest in the bare sand. The cockle *Cerastoderma glaucum*, the
263 polychaetes *Hediste diversicolor* and *Marenzelleria* spp., and mudsnails *Hydrobia* spp. had

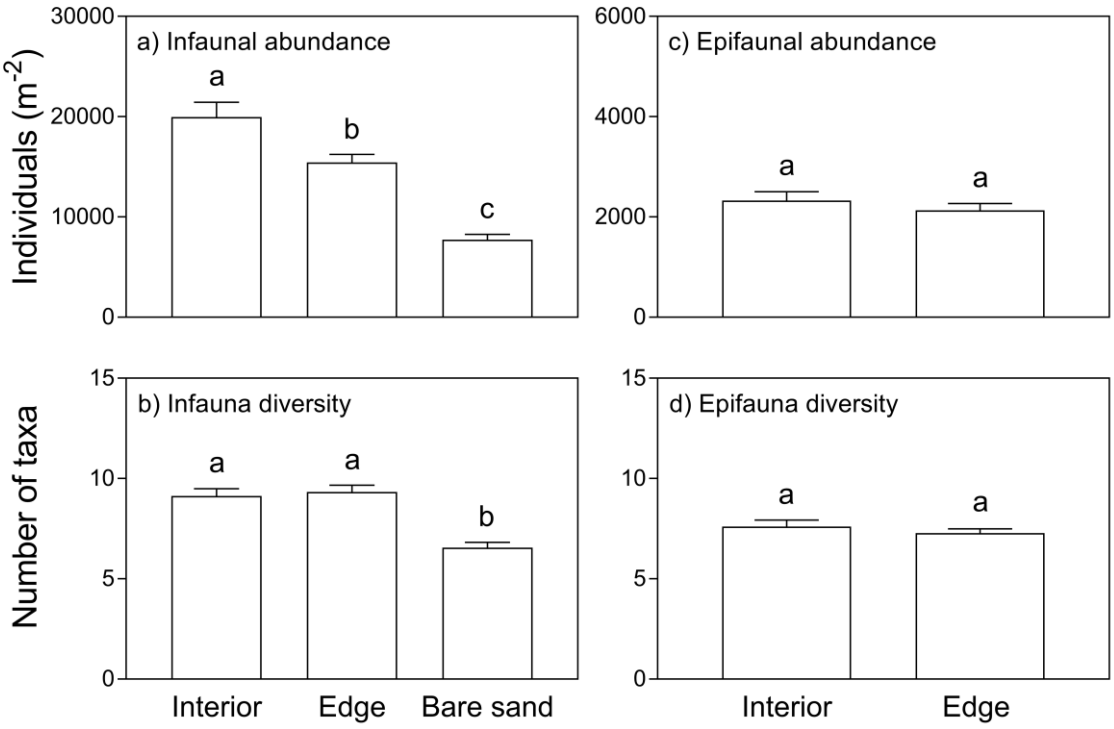
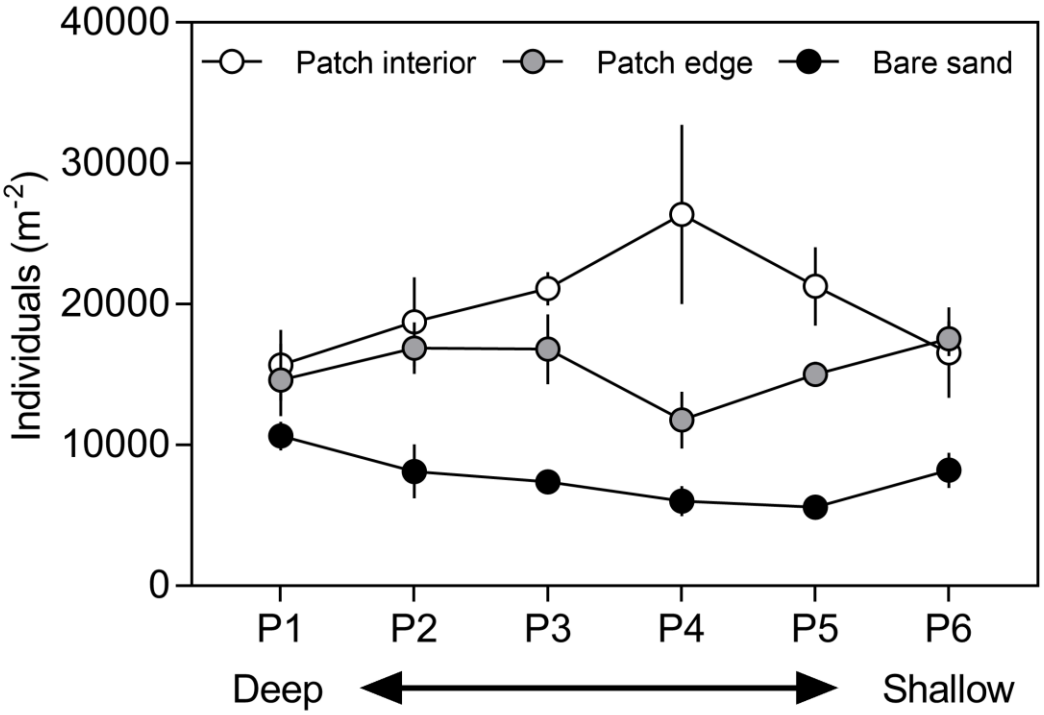


Figure 4. Mean abundance and diversity of infaunal (n=30 for Interior and Edge and n=29 for Bare sand) and epifaunal communities (n=18 for both Interior and Edge) ± SE. Different letters above bar plots indicate significant differences ($p < 0.05$).

significantly higher abundance in the *Zostera* than in the bare sand, but differences between *Zostera* interior and edge could not be detected for these taxa. Oligochaetes only showed significant differences between *Zostera* interior and the bare sand. The amphipod *Corophium volutator* was absent in the bare sand, although mean abundance did not differ significantly between the interior and edge. The bivalve *Macoma balthica* showed no differences between the habitats. Taxa-specific abundances are summarized in Appendix Fig. A1.

When examined for each patch individually, total infauna abundance in the *Zostera* interior and the bare sand showed contrasting patterns (Fig. 5). Highest infauna abundance in bare sand was found adjacent to the deepest patch P1 and decreased continuously towards patch P5, followed by an increase at P6. On the contrary, infauna abundance in the *Zostera*



278

279 **Figure 5.** Mean infauna abundance ± SE at *Zostera* patch interior, *Zostera* patch edge
280 and adjacent bare sediments along the depth gradient.

281 interior was lowest at P1. With decreasing depth, abundance increased, reaching a maximum
282 at patch P4, followed by a decrease for P5 and P6. Infauna abundance at the *Zostera* edge was
283 similar to the *Zostera* interior in the shallow and deep parts but decreased at intermediate
284 depths with the minimum at P4.

285 Mean abundance and number of taxa of leaf epifauna did not differ between edge and
286 interior (Fig. 4c, d). Further analysis of abundant epifaunal taxa revealed that only the snail
287 *Potamopygrus antipodarum* and the isopod *Idotea balthica* (Appendix Fig. A2) showed
288 significant differences between habitats, with a higher abundance of *P. antipodarum* in the
289 interiors, but higher abundance of *I. balthica* along the edges.

290 Abundance of epi- and infauna at the six sampling depths could be related to distinct
291 sediment and plant characteristics (Appendix Table A3). The relation to those variables,
292 however, differed considerably, depending on the habitat type. Infaunal abundance in the bare
293 sand correlated negatively with very coarse sand (r^2=0.268, $p<0.004$) and positively with

294 organic content (r^2=0.205, p<0.014). Infauna abundance at the patch interior in contrast,
295 increased with very coarse sand (r^2=0.157, p<0.030) and infauna at the patch edge was not
296 related to any sediment characteristics. Linear regression further indicated that infaunal total
297 abundance was not related to any plant characteristics, neither in the *Zostera* patch interior,
298 nor along the patch edges.
299 Epifauna at the patch edges increased with proportion of fine sand (r^2=0. 451, p=0.002)
300 and organic content (r^2=0.570, p<0.001), but decreased with very coarse sand (r^2=0.464,
301 p=0.002), while the epifauna abundance at the patch interior showed no correlation with
302 sediment characteristics. Instead, epifauna abundance at the interior was positively correlated
303 with shoot density (r^2=0.230, p<0.044) and above-ground biomass (r^2=0.234, p<0.042), while
304 edge epifauna showed no correlation with plant variables.
305
306 *3.4.Facilitation along the disturbance gradient*
307 The PCA, used to characterise the exposure gradient, could explain 79.6 % of the
308 variance on the two first axes (Fig. 6). When considered as stand-alone approximations, all
309 variables suggested an increase in physical exposure towards the same direction along
310 component 1 (50.2 %). This pattern indicates the representativeness of this component as a
311 proxy of exposure. Ripple index (-0.49) and d_{50} (0.57) showed strongest correlation with PC1,
312 while % fine sand (-0.34) had the lowest explanation on PC1. Consequently, we used a stress
313 gradient based on the scores from PC1 for further analyses. According to this proxy, exposure
314 increased along the sampling transect from P1 to P4 and declined again towards P6.
315 Linear regression revealed that none of the plant variables (shoot density, AB, BB, shoot
316 length) were related to the exposure gradient (as described by the PC 1), neither at the patch
317 interior nor at the patch edge. However, both in- and epifauna showed, depending on the
318 habitat position, different responses to physical exposure. Sediment infauna abundance in the

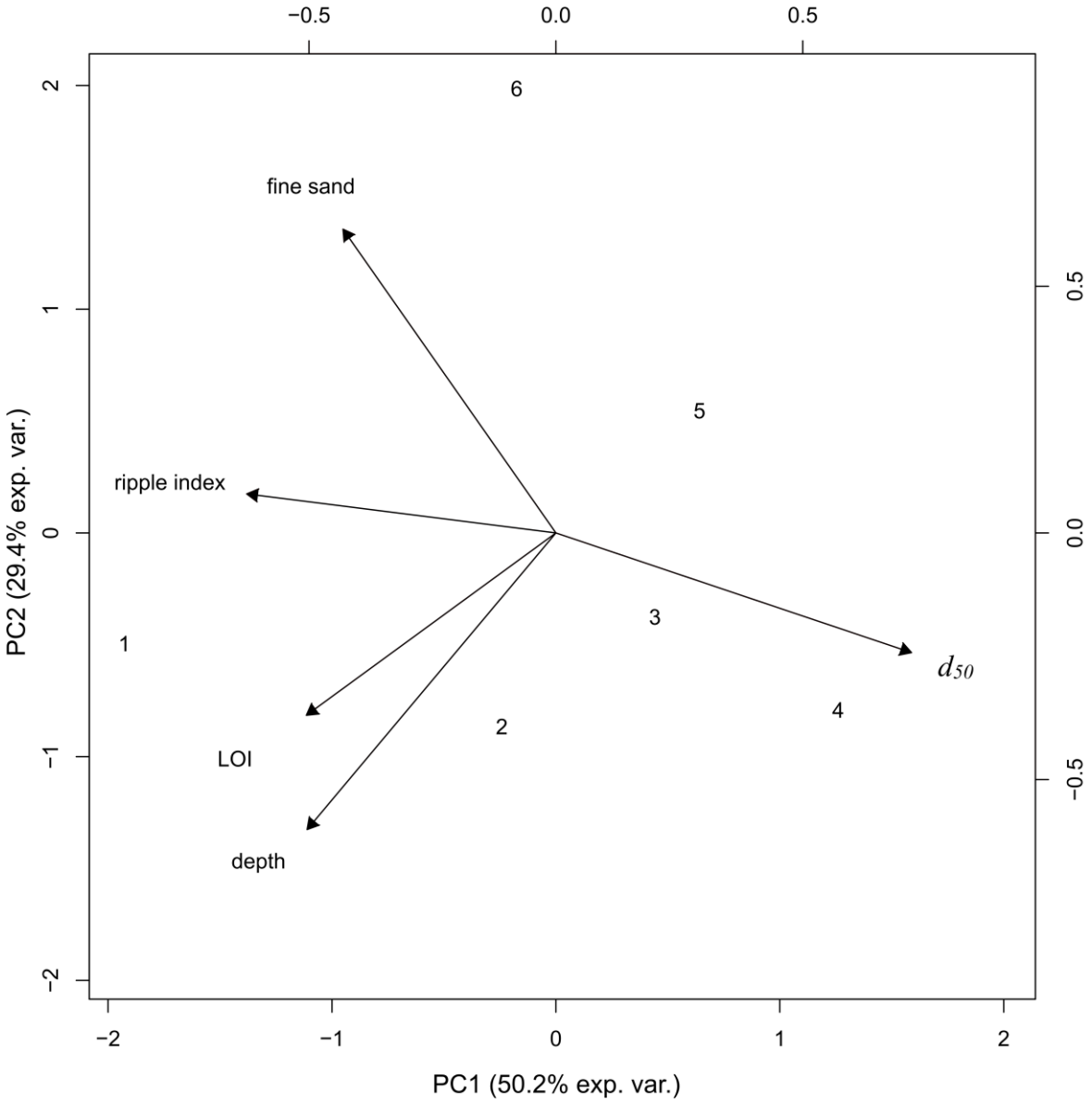
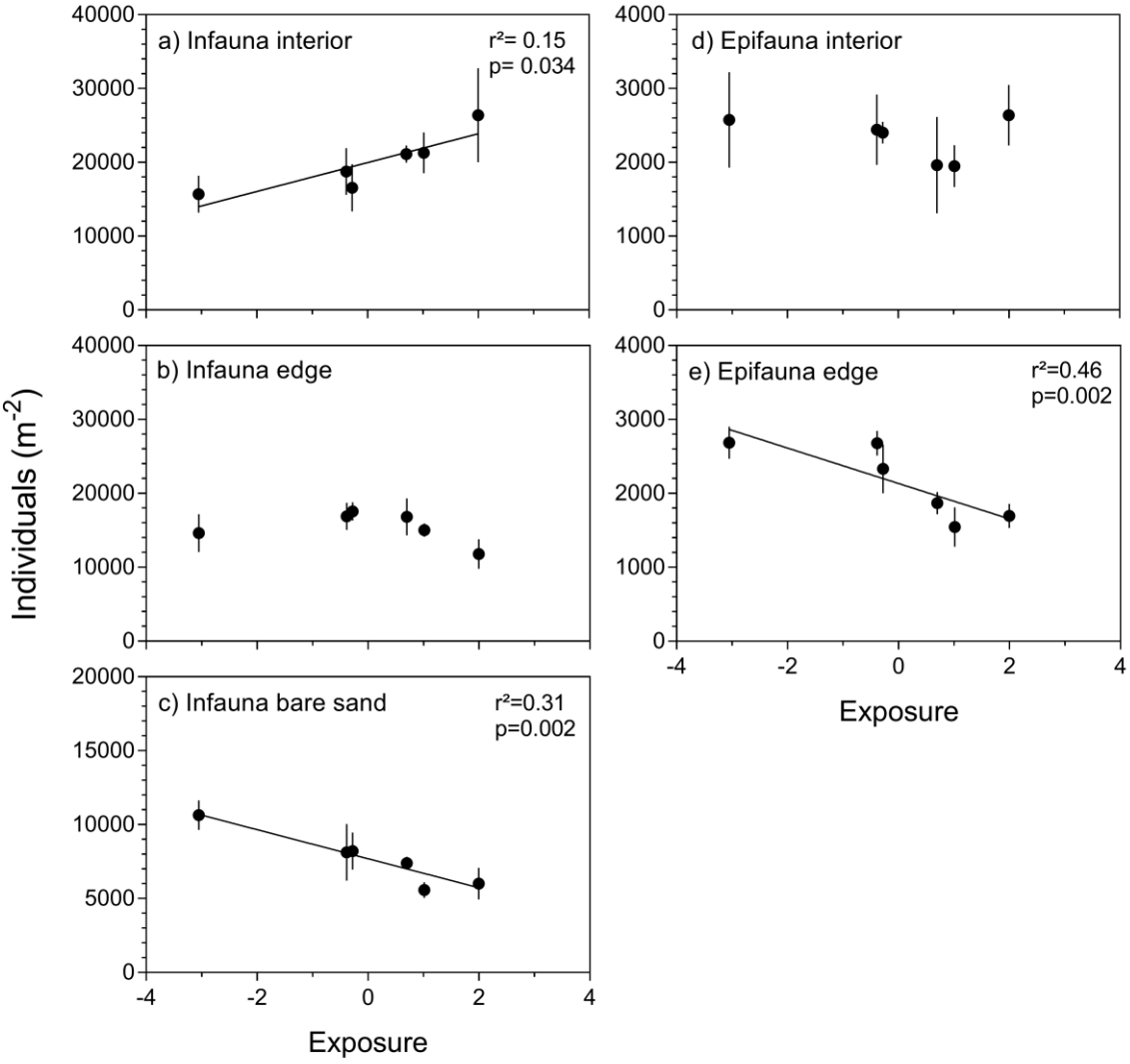


Figure 6. Principal component analysis of sediment parameters (% fine sand, % organic content and d_{50}), depth and ripple index adjacent to the six *Zostera* patches.

bare sand habitat was negatively correlated with physical exposure (Fig. 7a; r^2=0.31; p=0.002). In contrast, infauna at the *Zostera* interior correlated weakly, but positively with physical stress (Fig. 7c; r^2=0.15; p=0.034). Infauna along the *Zostera* edge showed no correlation with PC1 (Fig. 7b). Leaf epifaunal abundance at the *Zostera* edge was negatively correlated with the exposure proxy (Fig. 7e; r^2=0.46; p=0.002), whereas no correlation could be detected for epifauna in the interior of the seagrass patches (Fig. 7d).



328

329 **Figure 7.** Linear regression of total abundance along the exposure gradient, as described
330 by PC1, for the infaunal community at a) the *Zostera* interior, b) the *Zostera* edge and c)
331 the adjacent bare sand; and for the epifaunal community at d) the *Zostera* interior and e)
332 the *Zostera* edge. Regression line and corresponding r^2 and p-values are given where
333 linear regression analysis indicated a significant effect. Samples are shown as mean ±
334 SE.

335 While the overall patterns of infauna abundance across the exposure gradient are
336 relatively weak with low explanatory power (albeit significant), an interesting pattern emerges
337 when the ratio of the *Zostera* interior to bare sand abundance, i.e. the relative facilitation
338 ability of *Zostera*, is examined. Linear regression implied that exposure had strong positive
339 effects on the relative facilitation of *Zostera* (r^2=0.82, p=0.014, Fig. 8a). Interior infaunal

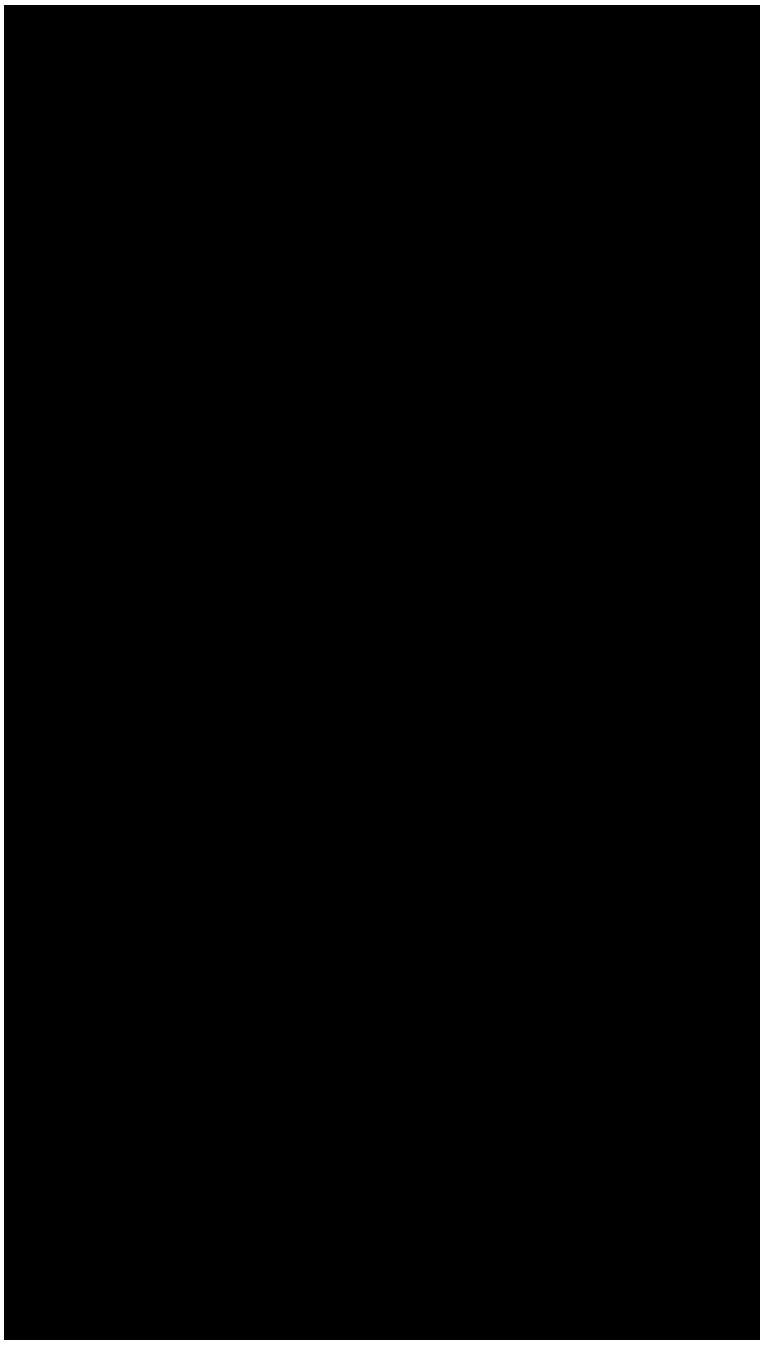


Figure 8. Linear regression of the ratio of *Zostera* interior (I) and bare sand (B) infauna a) abundance and b) diversity along the exposure gradient (as described by PC1).

abundance at the benign end of the stress gradient was about 1.5 fold the abundance at the adjacent bare sand, but reached almost 4.5 fold bare sand abundance at the stressful end of the gradient. The ratio of taxonomic richness on the other hand did not linearly increase along the gradient (r^2=0.43, p=0.156, Fig. 8b), but was overall higher at high compared to low exposure.

347 SIMPER analysis revealed that community dissimilarity between the *Zostera* patch
348 interior and the bare sand was higher at each of the six *Zostera* patches compared to
349 dissimilarities between the edge and the bare sand community, and in particular between the
350 interior and the edge community (Appendix Fig. A3). Taxa contributing most to the overall
351 dissimilarity between interior and bare sand across the entire gradient (46 % dissimilarity)
352 were *P. elegans* (14.2%), *Hydrobia* spp. (11.9 %) and Oligochaeta (11.1 %); all more
353 abundant at the patch interior; (Appendix Table A4). More importantly, the dissimilarity in
354 community composition between patch interior and bare sand significantly increased along
355 the physical stress gradient from 39 % to over 53 % (r^2=0.67, p=0.046, Fig. 8c, Appendix Fig.
356 A4). The taxa contributing most to the dissimilarity between interior and bare sand at the
357 stressful end of the gradient at P4 (53.5 % dissimilarity) were *C. volutator* (15.6 %), *Hydrobia*
358 spp. (14.7 %) and Oligochaeta (13.8 %); all more abundant in the *Zostera* interior; (Appendix
359 Table A3). Comparing the infaunal community of the *Zostera* interior between the benign and
360 stressful end furthermore showed that while *C. volutator* (16.7 % dissimilarity between P1
361 and P4), Oligochaeta (13.4 %) and *Hydrobia* spp. (7.7 %) were more abundant, *P.*
362 *antipodarum* (11.2%) was less abundant under physical stress (Appendix Table A3). On
363 average, dissimilarity between the six patches was significantly higher for the bare sand
364 infauna community (43.01 %), compared to the infauna in the patch interior (35.70 %,
365 p<0.0001) and the patch edge (33.55 %, p<0.0001, Appendix Table A5). Furthermore,
366 similarity between replicates within the patches was significantly higher in the patch interior
367 (66.14 %, p=0.049) and the patch edge (68.14 %, p= 0.008), compared to the bare sand (60.48
368 %, Appendix Table A5).
369
370 4. DISCUSSION
371 We examined how the foundation species *Zostera marina* promotes its associated
372 invertebrate community along a physical stress gradient. Our results emphasize the general

relevance of an aquatic engineering plant species for sediment fauna through habitat amelioration and reveal insights into the underlying conditionality. Consistent with past studies, we could find that infauna abundance and taxonomic richness were generally higher in *Zostera* than in nearby unvegetated sediments (Boström and Bonsdorff 1997, Fredriksen et al. 2010). Total abundance thereby increased towards the interior of the *Zostera* patches, and did not show, like occasionally demonstrated, an edge effect, i.e. elevated abundance close to the edges (Bowden et al. 2001, Bologna and Heck 2002). Besides habitat quality, physical disturbance is a crucial mechanism for structuring benthic communities (Probert 1984, Widdicombe and Austen 2001). An approximation for patch-specific exposure was derived by principle component analysis (PCA) of environmental variables likely correlated with hydrodynamic conditions. As shown by studies before, our results indicated that infauna abundance in unvegetated sediments was negatively affected by increasing exposure, waves and currents (Bonsdorff et al. 1995, Valanko et al. 2010). Ecosystem engineers, however, are assumed to increase the realized niche of associated communities (Bruno et al. 2003). In accordance with previous work, we could demonstrate the ameliorating effect of seagrass on hydrodynamics for its associated fauna (Irlandi 1996). The infauna abundance inside *Zostera* patches showed no decline along the exposure gradient, rather our results suggested an increase in abundance with increasing exposure. The relative importance of facilitation by *Zostera* becomes explicit, when directly comparing the infauna community in vegetated and unvegetated sediments. We found that the ratio of *Zostera* interior and bare sand infauna abundance increased monotonically from 1.5 to 4.5 along the gradient of increasing physical exposure. SIMPER analysis showed that simultaneously dissimilarity in community composition between interior and bare sand increased. This implies that not only single species are affected by facilitation, rather it can be inferred that *Zostera* facilitates its whole associated infaunal community through stress amelioration. Thereby, the average community similarity between patches, and between replicates within

patches, was significantly higher in both *Zostera* patch interior and *Zostera* patch edge compared to the bare sand. Thus, the increase in physical stress not just causes a decrease in total abundance, but also alters the infauna community structure in the unprotected bare sand. Through the shelter provided by *Zostera*, on the other hand, the infauna community composition remains comparably stable along the stress gradient.

Gradient approaches are often used where methods of simple patch-mosaic models (e.g. ANOVA) are not appropriate to capture the variability of environmental parameters, e.g. along depth or concentration gradients (McGarigal and Cushman 2005, Hewitt et al. 2007, Cushman et al. 2010). Besides the drawbacks of being of correlative nature and thus lacking direct manipulation, they can be a strong tool revealing insights in underlying functional relations between environmental and community data and related time integrated effects (Hewitt et al. 2007).

Contrary to our predictions, the PCA of environmental parameters along the depth gradient indicated that the realised exposure was not solely dependent on depth, but rather peaked at intermediate depth levels, suggesting a dampening of wave-exposure closer to the shore by the extensive *Zostera* meadows. The distribution of bare sand infauna abundance, i.e. a latent variable for an indirect gradient between more and less favourable conditions (ter Braak and Prentice 1988), matches the approximation of PC1 as an environmental stress gradient for the sediment infaunal community. Overall, other environmental variables such as temperature or light availability are unlikely to cause the observed contrast between bare sand and vegetation, as both are assumed to be highly correlated with depth, yet the exposure proxy deviates from the depth gradient. Moreover, the amelioration effect of *Zostera* on these drivers is limited. Turbidity through sediment resuspension is typically linked to hydrodynamics, and a reduced turbidity within the vegetated patches therefore can be seen as a by-product of the amelioration of hydrodynamics by *Zostera*. Furthermore, the depth differences in this study were limited and thus unlikely to affect other potential causes

425 such as faunal recruitment patterns of single species. Nonetheless, a positive impact on
426 recruitment success (i.e. increased juvenile survival through mitigation of physical stress) is
427 a facilitative outcome of seagrasses itself.

428 Although the outcome of facilitative interactions is highly dependent on local abiotic
429 and biotic conditions in any ecological community (Bertness and Callaway 1994, Lenihan
430 1999, Bruno and Bertness 2001), only a few studies have actually demonstrated this for
431 habitat engineers and their effect on associated communities (Norkko et al. 2006, Wright et
432 al. 2006, Lohrer et al. 2013, Watt and Scrosati 2013, Crotty and Bertness. 2015, McAfee et
433 al. 2016). These examples represent a broad range of different habitats and community types
434 such as marine habitat-forming benthic suspension feeders, intertidal rocky shore seaweeds
435 and cobble beach cord grasses or shrub mounds in terrestrial deserts. Importantly, however,
436 we show for the first time, in a subtidal soft-bottom setting, how amelioration effects are
437 modified by environmental variables related to hydrodynamic exposure. Our overall finding
438 of an increase of the relative importance of facilitation with increasing environmental stress
439 was thereby consistent with results from empirical studies on interspecific (e.g., Callaway et
440 al. 2002, Bennett et al. 2015, López et al. 2016), conspecific (e.g., Bennett et al. 2015, Yang
441 et al. 2016) and trophic (e.g., Daleo and Iribarne 2009) interactions and gives further insights
442 to community-wide effects of habitat engineers in marine environments (McAfee et al. 2016,
443 Watt and Scrosati 2013).

444 This study further highlights how environmental conditions can affect the relationship
445 between a foundation species and its associated community differently depending on the
446 faunal assemblage in question and proximity to habitat edges. Contrasting to the *Zostera*
447 interior community, infauna living at the habitat edge did not linearly increase with exposure.
448 Instead our results show a decline at high exposure rates, indicating that here a threshold in
449 physical conditions has been reached, at which *Zostera* edges are unable to provide suitable
450 habitat for infauna. Similarly, mobile leaf epifauna declined in abundance with increasing

exposure along the *Zostera* edges, while epifauna was unaffected in the *Zostera* interior. Although in a different setting, exploring facilitation in mussel beds through amelioration of temperature effects, Jurgens and Gaylord (2016) demonstrated that stress amelioration by foundation species can be highly variable within single habitat patches and can even shift to exacerbation at habitat edges. This points out that, depending on underlying abiotic and biotic conditions, an increase of relative importance of facilitation towards stressful environments is not always necessarily true, see Norkko et al. (2006), Kawai and Tokeshi (2007), Fugère et al. (2012), Bakker et al. (2013), Castanho and Prado (2014).

Our results further give indication of mechanisms responsible for the facilitative effect of the foundation species *Zostera*. We have shown that relative facilitation of *Zostera* was not due to changes in structural complexity of the *Zostera* patches per se; i.e. infauna abundance was not correlated with any plant variables. Besides the positive correlation of *Zostera* infauna with exposure was rather week (r^2=0.15), compared to the negative correlation of infauna in the unvegetated sediments (r^2=0.31). This indicates that the facilitative effect is first of all attributed to a sheltering potential of *Zostera* along the exposure gradient, i.e. reduction in wave disturbance and current flow, expressed by decreasing sediment grain size and trapping of organic particles towards the patch interior (Boström and Bonsdorff 1997, Hendriks et al. 2008).

Epifauna abundance on the other hand did increase with shoot density and above ground biomass at the *Zostera* interior. This underlines the major relevance of seagrass habitat complexity for epifaunal communities (Boström and Bonsdorff 1997, Carr et al. 2011). However, this pattern was not detected at the edges, where shoot density and above-ground biomass had no effect on epifaunal abundance. Here, total abundance was primarily driven by sediment characteristics, with lowest total abundance at low organic content and high proportion of very coarse sand, further suggesting that close to the edge the occurrence of strong physical forces exceeds the sheltering capacity of *Zostera*.

Habitat edges are defined as sudden transitions between adjacent habitats and play a major role in structuring ecological communities (Strayer et al. 2003). Our results indicate that seagrass patch edges can considerably buffer hydrodynamic forcing (Fonseca et al. 1982, Gambi et al. 1990, Peterson et al. 2004, Temmerman et al. 2005). The substantial changes in hydrodynamic variables, but also biological processes (Boström et al. 2006) that interact at the edges of seagrass patches, influence e.g. recruitment patterns (Carroll et al. 2012) and distributions of predators and prey (Macreadie et al. 2010, González-Ortiz et al. 2014). Seagrass patches have erratically been associated with positive edge effects (Tanner 2005), expressed as an increase in species abundance or diversity (Bowden et al. 2001, Ries et al. 2004, Bologna and Heck 2002, Connolly and Hindell 2006). In this study, however, only the isopod *I. balthica* showed elevated abundances at the edges, implying that edge effects are highly species specific (Tanner 2005), and dependent on environmental context (e.g., hydrodynamic regime).

It has been shown that environmental stress or an additional engineering species can reduce and even inhibit the facilitative relevance of a marine ecosystem engineer for its associated community (Norkko et al. 2006, Lohrer et al. 2013, McAffee et al. 2016). We could demonstrate that underlying mechanisms of facilitation depended on within-habitat position and the faunal assemblage in question. Specifically, we demonstrated strong differences between epifaunal and infaunal assemblages due to different positive feedback mechanisms (Maxwell et al. 2017). Our findings have direct implications particularly for management efforts in degrading biogenic habitats. The ongoing loss of seagrass habitats worldwide (Waycott et al. 2009) and the limited success of restoration programs (van Katwijk et al. 2016) calls for a widespread and sustainable management of these critically important habitats. The results of this study emphasize that conservation efforts should focus particularly on physically stressful environments, as the ecological value in promoting associated communities by seagrass meadows is assumed to be most pronounced here. In line

503 with these findings, we encourage further experimental efforts to reveal the conditional
504 outcome of facilitation, including both interior and edge habitats for a broad range of
505 foundation species.
506
507 ACKNOWLEDGEMENTS
508 This study was funded by the Academy of Finland (project numbers 114076 and 110999,
509 294853, to AN, JN), the Functional Marine Biodiversity Network (FunMarBio) at Åbo
510 Akademi University (LM) and the Schure Beijerinck Popping Fonds (travel grant
511 SBP/JK/2008-33, TY, FM). We would like to thank Tvärminne Zoological Station for
512 providing facilities and logistic support.
513
514 AUTHORS CONTRIBUTIONS
515 A.N., J.N., T.Y. designed the study; A.N., J.N., T.Y, F.M., S.V., A.J., A.V. performed field
516 sampling; A.J., A.V., J.N., S.V. performed laboratory analysis;
517 L.M. analyzed the data; L.M. drafted the manuscript with substantial input by C.B. and A.N.;
518 T.Y., A.J., F.M., S.V., A.V., C.B., J.N. and A.N. commented and revised the manuscript.
519
520 LITERATURE CITED
521 Bakker, E.S., Dobrescu, I., Straile, D., Holmgren, M., 2013. Testing the stress gradient
522 hypothesis in herbivore communities: facilitation peaks at intermediate nutrient levels.
523 Ecology 94, 1776–1784. https://doi.org/10.1890/12-1175.1
524 Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M.,
525 Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F.,
526 Weinstein, M.P., 2001. The Identification, Conservation, and Management of Estuarine
527 and Marine Nurseries for Fish and InvertebratesA better understanding of the habitats
528 that serve as nurseries for marine species and the factors that create site-specific

variability in nursery quality will improve conservation and management of these areas. BioScience 51, 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Bennett, S., Wernberg, T., 2014. Canopy facilitates seaweed recruitment on subtidal temperate reefs. J Ecol 102, 1462–1470. https://doi.org/10.1111/1365-2745.12302

Bennett, S., Wernberg, T., de Bettignies, T., Kendrick, G.A., Anderson, R.J., Bolton, J.J., Rodgers, K.L., Shears, N.T., Leclerc, J.-C., Lévêque, L., Davoult, D., Christie, H.C., 2015. Canopy interactions and physical stress gradients in subtidal communities. Ecol Lett 18, 677–686. https://doi.org/10.1111/ele.12446

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends in Ecology & Evolution 9, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bologna, P.A., Heck, K.L., 2002. Impact of habitat edges on density and secondary production of seagrass-associated fauna. Estuaries 25, 1033–1044.

Bonsdorff, E., Norkko, A., Sandberg, E., 1995. Structuring zoobenthos: the importance of predation, siphon cropping and physical disturbance. J.Exp.Mar.Biol.Ecol. 192, 125–144.

Boström, C., Baden, S., Bockelmann, A.-C., Dromph, K., Fredriksen, S., Gustafsson, C., Krause-Jensen, D., Möller, T., Nielsen, S.L., Olesen, B., Olsen, J., Pihl, L., Rinde, E., 2014. Distribution, structure and function of Nordic eelgrass (Zostera marina) ecosystems: implications for coastal management and conservation. Aquatic Conserv: Mar. Freshw. Ecosyst. 24, 410–434. https://doi.org/10.1002/aqc.2424

Boström, C., Bonsdorff, E., 1997. Community structure and spatial variation of benthic invertebrates associated with Zostera marina (L.) beds in the northern Baltic Sea. Journal of Sea Research 37, 153–166. https://doi.org/10.1016/S1385-1101(96)00007-X

Boström, C., Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine, Coastal and Shelf Science, Ecological and

555 Management Implications on Seagrass Landscapes 68, 383–403.
556 https://doi.org/10.1016/j.ecss.2006.01.026
557 Boström, C., Pittman, S.J., Simenstad, C., Kneib, R.T., 2011. Seascape ecology of coastal
558 biogenic habitats:: advances, gaps, and challenges. Marine Ecology Progress Series 427,
559 191–218.
560 Bowden, D.A., Rowden, A.A., Attrill, M.J., 2001. Effect of patch size and in-patch location
561 on the infaunal macroinvertebrate assemblages of Zostera marina seagrass beds.
562 J.Exp.Mar.Biol.Ecol. 259, 133–154.
563 Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G.,
564 Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket,
565 E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L.,
566 Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in
567 plant communities: the past, the present, and the future. Journal of Ecology 96, 18–34.
568 https://doi.org/10.1111/j.1365-2745.2007.01295.x
569 Bruno, J., Bertness, M., 2001. Positive interactions, facilitations and foundation species.
570 Marine community ecology.Sinauer Associates, Inc Publishers, Sunderland,
571 Massachusetts 201–218.
572 Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological
573 theory. Trends in Ecology & Evolution 18, 119–125. https://doi.org/10.1016/S0169-
574 5347(02)00045-9
575 Bulleri, F., 2009. Facilitation research in marine systems: state of the art, emerging patterns
576 and insights for future developments. Journal of Ecology 97, 1121–1130.
577 https://doi.org/10.1111/j.1365-2745.2009.01567.x
578 Bulleri, F., Cristaudo, C., Alestra, T., Benedetti-Cecchi, L., 2011. Crossing gradients of
579 consumer pressure and physical stress on shallow rocky reefs: a test of the stress-

gradient hypothesis. Journal of Ecology 99, 335–344. https://doi.org/10.1111/j.1365-2745.2010.01750.x

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844–848. https://doi.org/10.1038/nature00812

Carr, L.A., Boyer, K.E., Brooks, A.J., 2011. Spatial patterns of epifaunal communities in San Francisco Bay eelgrass (Zostera marina) beds. Marine Ecology 32, 88–103. https://doi.org/10.1111/j.1439-0485.2010.00411.x

Carroll, J.M., Furman, B.T., Tettelbach, S.T., Peterson, B.J., 2012. Balancing the edge effects budget: bay scallop settlement and loss along a seagrass edge. Ecology 93, 1637–1647. https://doi.org/10.1890/11-1904.1

Castanho, C. de T., Prado, P.I., 2014. Benefit of Shading by Nurse Plant Does Not Change along a Stress Gradient in a Coastal Dune. PLOS ONE 9, e105082. https://doi.org/10.1371/journal.pone.0105082

Clarke, K.R., Gorley, R.N., 2006. PRIMER V6: user manual-tutorial.

Clifton, H.E., Dingler, J.R., 1984. Wave-formed structures and paleoenvironmental reconstruction. Marine Geology, Hydrodynamics and Sedimentation in Wave-Dominated Coastal Environments 60, 165–198. https://doi.org/10.1016/0025-3227(84)90149-X

Connolly, R.M., Hindell, J.S., 2006. Review of nekton patterns and ecological processes in seagrass landscapes. Estuarine, Coastal and Shelf Science, Ecological and Management Implications on Seagrass Landscapes 68, 433–444. https://doi.org/10.1016/j.ecss.2006.01.023

Cordero, A.L.H., Seitz, R.D., Lipcius, R.N., Bovery, C.M., Schulte, D.M., 2012. Habitat Affects Survival of Translocated Bay Scallops, Argopecten irradians concentricus (Say

606 1822), in Lower Chesapeake Bay. Estuaries and Coasts 35, 1340–1345.
607 https://doi.org/10.1007/s12237-012-9510-2
608 Crotty, S.M., Bertness, M.D., 2015. Positive interactions expand habitat use and the realized
609 niches of sympatric species. Ecology 96, 2575–2582. https://doi.org/10.1890/15-0240.1
610 Cushman, S.A., Gutzweiler, K., Evans, J.S., McGarigal, K., 2010. The gradient paradigm: a
611 conceptual and analytical framework for landscape ecology, in: Spatial Complexity,
612 Informatics, and Wildlife Conservation. Springer, pp. 83–108.
613 Daleo, P., Iribarne, O., 2009. Beyond competition: the stress-gradient hypothesis tested in
614 plant–herbivore interactions. Ecology 90, 2368–2374. https://doi.org/10.1890/08-2330.1
615 Dayton, P.K., 1972. Toward an understanding of community resilience and the potential
616 effects of enrichments to the benthos at McMurdo Sound, Antarctica. Presented at the
617 Proceedings of the colloquium on conservation problems in Antarctica, Allen Press
618 Lawrence, Kansas, USA, pp. 81–96.
619 Elliott, M., Nedwell, S., Jones, N., Read, S., Cutts, N., Hemingway, K., 1998. Volume II
620 Intertidal Sand and Mudflats & Subtidal Mobile Sandbanks. An overview of dynamic
621 and sensitivity characteristics for conservation management of marine SACs. UK
622 Marine SACs Project.
623 Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R.,
624 Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse,
625 N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle,
626 B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and
627 dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479–
628 486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2
629 Fonseca, M.S., Cahalan, J.A., 1992. A preliminary evaluation of wave attenuation by four
630 species of seagrass. Estuarine, Coastal and Shelf Science 35, 565–576.
631 https://doi.org/10.1016/S0272-7714(05)80039-3

632 Fonseca, M.S., Fisher, J.S., Zieman, J.C., Thayer, G.W., 1982. Influence of the seagrass,
633 Zostera marina L., on current flow. Estuarine, Coastal and Shelf Science 15, 351–364.
634 https://doi.org/10.1016/0272-7714(82)90046-4
635 Fredriksen, S., De Backer, A., Boström, C., Christie, H., 2010. Infauna from Zostera marina
636 L. meadows in Norway. Differences in vegetated and unvegetated areas. Marine biology
637 research 6, 189–200.
638 Fugère, V., Andino, P., Espinosa, R., Anthelme, F., Jacobsen, D., Dangles, O., 2012. Testing
639 the stress-gradient hypothesis with aquatic detritivorous invertebrates: insights for
640 biodiversity-ecosystem functioning research. Journal of Animal Ecology 81, 1259–
641 1267. https://doi.org/10.1111/j.1365-2656.2012.01994.x
642 Gallagher, E.D., Jumars, P.A., Trueblood, D.D., 1983. Facilitation of soft-bottom benthic
643 succession by tube builders. Ecology 64, 1200–1216. https://doi.org/10.2307/1937829
644 Gambi, M.C., Nowell, A.R.M., Jumars, P.A., 1990. Flume observations on flow dynamics in
645 Zostera marina (eelgrass) beds. Marine Ecology Progress Series 61, 159–169.
646 González-Ortiz, V., Egea, L.G., Jiménez-Ramos, R., Moreno-Marín, F., Pérez-Lloréns, J.L.,
647 Bouma, T., Brun, F., 2016. Submerged vegetation complexity modifies benthic infauna
648 communities: the hidden role of the belowground system. Mar Ecol 37, 543–552.
649 https://doi.org/10.1111/maec.12292
650 González-Ortiz, V., Egea, L.G., Jiménez-Ramos, R., Moreno-Marín, F., Pérez-Lloréns, J.L.,
651 Bouma, T.J., Brun, F.G., 2014. Interactions between Seagrass Complexity,
652 Hydrodynamic Flow and Biomixing Alter Food Availability for Associated Filter-
653 Feeding Organisms. PLOS ONE 9, e104949.
654 https://doi.org/10.1371/journal.pone.0104949
655 Gray, J.S., Elliott, M., 2009. Ecology of marine sediments: from science to management.
656 Oxford University Press.

He, Q., Bertness, M.D., Altieri, A.H., 2013. Global shifts towards positive species interactions with increasing environmental stress. Ecol Lett 16, 695–706. https://doi.org/10.1111/ele.12080

Heck Jr., K.L., Orth, R.J., 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages, in: Kennedy, V.S. (Ed.), Estuarine Perspectives. Academic Press, pp. 449–464. https://doi.org/10.1016/B978-0-12-404060-1.50043-5

Hendriks, I.E., Sintes, T., Bouma, T.J., Duarte, C.M., 2008. Experimental assessment and modeling evaluation of the effects of the seagrass Posidonia oceanica on flow and particle trapping. Marine Ecology Progress Series 356, 163–173.

Hewitt, J.E., Thrush, S.F., Dayton, P.K., Bonsdorff, E., 2007. The Effect of Spatial and Temporal Heterogeneity on the Design and Analysis of Empirical Studies of Scale-Dependent Systems. The American Naturalist 169, 398–408. https://doi.org/10.1086/510925

Holmgren, M., Scheffer, M., 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. Journal of Ecology 98, 1269–1275. https://doi.org/10.1111/j.1365-2745.2010.01709.x

Irlandi, E.A., 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve [WWW Document]. https://doi.org/info:doi/10.1357/0022240963213439

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as Ecosystem Engineers, in: Ecosystem Management. Springer New York, pp. 130–147. https://doi.org/10.1007/978-1-4612-4018-1_14

Jurgens, L.J., Gaylord, B., 2016. Edge effects reverse facilitation by a widespread foundation species. Sci Rep 6. https://doi.org/10.1038/srep37573

682 Kawai, T., Tokeshi, M., 2007. Testing the facilitation–competition paradigm under the stress-
683 gradient hypothesis: decoupling multiple stress factors. Proceedings of the Royal
684 Society of London B: Biological Sciences 274, 2503–2508.
685 https://doi.org/10.1098/rspb.2007.0871
686 Lenihan, H.S., 1999. Physical–Biological Coupling on Oyster Reefs: How Habitat Structure
687 Influences Individual Performance. Ecological Monographs 69, 251–275.
688 https://doi.org/10.1890/0012-9615(1999)069[0251:PBCOOR]2.0.CO;2
689 Lohrer, A.M., Rodil, I.F., Townsend, M., Chiaroni, L.D., Hewitt, J.E., Thrush, S.F., 2013.
690 Biogenic habitat transitions influence facilitation in a marine soft-sediment ecosystem.
691 Ecology 94, 136–145. https://doi.org/10.1890/11-1779.1
692 López, R.P., Squeo, F.A., Armas, C., Kelt, D.A., Gutiérrez, J.R., 2016. Enhanced facilitation
693 at the extreme end of the aridity gradient in the Atacama Desert: a community-level
694 approach. Ecology 97, 1593–1604. https://doi.org/10.1890/15-1152.1
695 Lortie, C.J., Callaway, R.M., 2006. Re-analysis of meta-analysis: support for the stress-
696 gradient hypothesis. Journal of Ecology 94, 7–16. https://doi.org/10.1111/j.1365-
697 2745.2005.01066.x
698 Macreadie, P.I., Hindell, J.S., Keough, M.J., Jenkins, G.P., Connolly, R.M., 2010. Resource
699 distribution influences positive edge effects in a seagrass fish. Ecology 91, 2013–2021.
700 https://doi.org/10.1890/08-1890.1
701 Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient
702 hypothesis for competition and facilitation in plant communities. Journal of Ecology 97,
703 199–205. https://doi.org/10.1111/j.1365-2745.2008.01476.x
704 Maestre, F.T., Valladares, F., Reynolds, J.F., 2005. Is the change of plant–plant interactions
705 with abiotic stress predictable? A meta-analysis of field results in arid environments.
706 Journal of Ecology 93, 748–757. https://doi.org/10.1111/j.1365-2745.2005.01017.x

Maxwell, P.S., Eklöf, J.S., van Katwijk, M.M., O'Brien, K.R., de la Torre-Castro, M., Boström, C., Bouma, T.J., Krause-Jensen, D., Unsworth, R.K.F., van Tussenbroek, B.I., van der Heide, T., 2017. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems – a review. Biol Rev 92, 1521–1538. https://doi.org/10.1111/brv.12294

McAfee, D., Cole, V.J., Bishop, M.J., 2016. Latitudinal gradients in ecosystem engineering by oysters vary across habitats. Ecology 97, 929–939. https://doi.org/10.1890/15-0651.1

McGarigal, K., Cushman, S., 2005. The gradient concept of landscape structure [Chapter 12]. In: Wiens, John A.; Moss, Michael R., eds. Issues and Perspectives in Landscape Ecology. Cambridge University Press. p. 112-119. 112–119.

Michalet, R., Pugnaire, F.I., 2016. Facilitation in communities: underlying mechanisms, community and ecosystem implications. Funct Ecol 30, 3–9. https://doi.org/10.1111/1365-2435.12602

Norkko, A., Hewitt, J.E., Thrush, S.F., Funnell, G.A., 2006. Conditional Outcomes of Facilitation by a Habitat-Modifying Subtidal Bivalve. Ecology 87, 226–234. https://doi.org/10.1890/05-0176

Peterson, C.H., Luettich, R.A., Micheli, F., Skilleter, G.A., 2004. Attenuation of water flow inside seagrass canopies of differing structure. Marine Ecology Progress Series 268, 81–92. https://doi.org/10.2307/24867608

Probert, P., 1984. Disturbance, sediment stability, and trophic structure of soft-bottom communities. J.Mar.Res. 42, 893–921.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ries, L., Robert J. Fletcher, J., Battin, J., Sisk, T.D., 2004. Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. Annual Review of Ecology,

732 Evolution, and Systematics 35, 491–522.
733 https://doi.org/10.1146/annurev.ecolsys.35.112202.130148
734 Samper-Villarreal, J., Lovelock, C.E., Saunders, M.I., Roelfsema, C., Mumby, P.J., 2016.
735 Organic carbon in seagrass sediments is influenced by seagrass canopy complexity,
736 turbidity, wave height, and water depth. Limnol.Oceanogr. 61, 938–952.
737 Sharma, S., Goff, J., Moody, R.M., Byron, D., Heck, K.L., Powers, S.P., Ferraro, C., Cebrian,
738 J., 2016. Do restored oyster reefs benefit seagrasses? An experimental study in the
739 Northern Gulf of Mexico. Restor Ecol 24, 306–313. https://doi.org/10.1111/rec.12329
740 Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A., Belnap, J., 2003. A Classification of
741 Ecological Boundaries. BioScience 53, 723–729. https://doi.org/10.1641/0006-
742 3568(2003)053[0723:ACOEB]2.0.CO;2
743 Tanner, J.E., 2005. Edge effects on fauna in fragmented seagrass meadows. Austral Ecology
744 30, 210–218. https://doi.org/10.1111/j.1442-9993.2005.01438.x
745 Temmerman, S., Bouma, T.J., Govers, G., Wang, Z.B., De Vries, M.B., Herman, P.M.J.,
746 2005. Impact of vegetation on flow routing and sedimentation patterns: Three-
747 dimensional modeling for a tidal marsh. J. Geophys. Res. 110, F04019.
748 https://doi.org/10.1029/2005JF000301
749 Ter Braak, C.J., Prentice, I.C., 1988. A theory of gradient analysis, in: Advances in Ecological
750 Research. Elsevier, pp. 271–317.
751 Valanko, S., Norkko, A., Norkko, J., 2010. Strategies of post-larval dispersal in non-tidal soft-
752 sediment communities. J.Exp.Mar.Biol.Ecol. 384, 51–60.
753 van Katwijk, M.M., Thorhaug, A., Marbà, N., Orth, R.J., Duarte, C.M., Kendrick, G.A.,
754 Althuizen, I.H.J., Balestri, E., Bernard, G., Cambridge, M.L., Cunha, A., Durance, C.,
755 Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K.-S.,
756 Meinesz, A., Nakaoka, M., O'Brien, K.R., Paling, E.I., Pickerell, C., Ransijn, A.M.A.,

Verduin, J.J., 2016. Global analysis of seagrass restoration: the importance of large-scale planting. J Appl Ecol 53, 567–578. https://doi.org/10.1111/1365-2664.12562

Watt, C.A., Scrosati, R.A., 2013. Bioengineer effects on understory species richness, diversity, and composition change along an environmental stress gradient: Experimental and mensurative evidence. Estuarine, Coastal and Shelf Science 123, 10–18. https://doi.org/10.1016/j.ecss.2013.02.006

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. PNAS 106, 12377–12381. https://doi.org/10.1073/pnas.0905620106

Wentworth, C.K., 1922. A Scale of Grade and Class Terms for Clastic Sediments. The Journal of Geology 30, 377–392. https://doi.org/10.1086/622910

Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., Staehr, P.A., Toohey, B.D., 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecology Letters 13, 685–694. https://doi.org/10.1111/j.1461-0248.2010.01466.x

Widdicombe, S., Austen, M.C., 2001. The interaction between physical disturbance and organic enrichment: an important element in structuring benthic communities. Limnol.Oceanogr. 46, 1720–1733.

Wright, J.P., Jones, C.G., Boeken, B., Shachak, M., 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. Journal of Ecology 94, 815–824. https://doi.org/10.1111/j.1365-2745.2006.01132.x

Woodin, S.A., 1981. Disturbance and Community Structure in a Shallow Water Sand Flat. Ecology 62, 1052–1066. https://doi.org/10.2307/1937004

Yang S, HilleRisLambers J, Ruesink JL, 2016. Reversal of intraspecific interactions by an ecosystem engineer leads to variable seedling success along a stress gradient. Mar Ecol Prog Ser 543, 163–171.

APPENDIX:

Table A1. Results of two-way ANOVA on sediment and plant characteristics with Patch (P1-P6) and Habitat (*Zostera* interior – *Zostera* edge – Bare sand) as main factors.

Class	Data set	Transformation	Source	Df	SS	MS	F	P
Sediment	Fine	no	Patch	5	0.07129	0.01426	12	**<0.0001**
			Habitat	2	0.1588	0.07938	66.79	**<0.0001**
			Patch × Habitat	10	0.03698	0.003698	3.112	**0.0024**
			Residuals	72	0.08557	0.001188		
	Medium	no	Patch	5	0.1857	0.03713	29.87	**<0.0001**
			Habitat	2	0.4259	0.213	171.3	**<0.0001**
			Patch × Habitat	10	0.03789	0.003789	3.047	**0.0028**
			Residuals	72	0.08952	0.001243		
	Coarse	no	Patch	5	0.09488	0.01898	8.252	**<0.0001**
			Habitat	2	0.03613	0.01806	7.855	**0.0008**
			Patch × Habitat	10	0.1248	0.01248	5.428	**<0.0001**
			Residuals	72	0.1656	0.002299		
	Very coarse	no	Patch	5	0.3499	0.06998	37.8	**<0.0001**
			Habitat	2	0.9959	0.498	269	**<0.0001**
			Patch × Habitat	10	0.08792	0.008792	4.749	**<0.0001**
			Residuals	72	0.1333	0.001851		
	Organics	no	Patch	5	0.016221	0.003244	14.005	**<0.0001**
			Habitat	2	0.02094	0.01047	45.198	**<0.0001**
			Patch × Habitat	10	0.005334	0.000533	2.303	**0.0211**
			Residuals	70	0.016215	0.000232		
Plant	Shoot density	no	Patch	5	181793	36359	1.922	0.1278
			Habitat	1	17885	17885	0.945	0.3406
			Patch × Habitat	5	248874	49775	2.631	**0.0493**
			Residuals	24	453982	18916		
	Above-ground biomass	Log+0.5	Patch	5	0.484	0.0968	0.677	0.6453
			Habitat	1	0.478	0.4781	3.343	0.08
			Patch × Habitat	5	2.067	0.4134	2.89	**0.0351**
			Residuals	24	3.433	0.143		
	Below-ground biomass	Log+0.5	Patch	5	1.517	0.3034	2.331	0.0736
			Habitat	1	2.3173	2.3173	17.799	**0.0003**
			Patch × Habitat	5	0.5374	0.1075	0.826	0.5439
			Residuals	24	3.1245	0.1302		
	Shoot length	no	Patch	5	1135.7	227.1	8.285	**0.0001**
			Habitat	1	533.2	533.2	19.45	**0.0002**
			Patch × Habitat	5	903.4	180.7	6.591	**0.0005**
			Residuals	24	658	27.4		

Table A2. Habitat (I=Interior, E=Edge, B=Bare sand) and means of grain size fractions (sand) 1-2mm (very coarse, %), 0.5-1mm (coarse, %), 0.25-0.5 (medium, %) and 0.1-0.25 (fine, %), organic content (LOI, %), *Zostera* shoot density (shoots m^{-2}), *Zostera* above- and belowground biomass (AB and BB, g DW m^{-2}), *Zostera* shoot length (shoot l, cm), depth (m), sand ripple height/length (ripples, mm) and median grain size (d_{50}, mm) at the sampling locations P1-6 and as average (Total). For overall effects between habitats, also significant differences are indicated by superscript letters, based on habitat effect of two-way ANOVA ($p < 0.05$).

Patch	Habitat	Grain size (mm)						d_{50}	LOI	Shoots	AB	BB	Shoot L	Depth	Ripples
		2.00	1.00	0.50	0.125	0.063	<0.063	(mm)	(%)	(m^{-2})	(g DW m^{-2})	(g DW m^{-2})	(cm)	(m)	l/h (mm)
	I	6.2‰	26.2‰	45.2‰	19.7‰	0.18‰	0.09‰	0.76	0.18	247.3	41.4	176.8	35.8		
P1	E	8.3‰	41.6‰	43.9‰	7.2‰	0.01‰	0.01‰	0.98	0.14	328.0	39.5	76.6	40.6		
	B	22.6‰	36.4‰	28.9‰	2.4‰	0.00‰	0.00‰	1.33	0.14					4.1	32.4/5.1
	I	10.7‰	41.2‰	39.9‰	7.1‰	0.05‰	0.02‰	1.04	0.15	338.1	42.2	127.0	52.6		
P2	E	9.6‰	37.9‰	42.4‰	7.1‰	0.03‰	0.03‰	0.99	0.15	519.8	64.3	110.9	53.5		
	B	31.9‰	28.3‰	23.9‰	0.7‰	0.00‰	0.00‰	1.51	0.12					3.8	35.0/6.7
	I	12.2‰	40.3‰	41.5‰	8.9‰	0.07‰	0.03‰	0.97	0.16	363.4	56.1	135.5	57.5		
P3	E	24.5‰	40.2‰	33.2‰	3.1‰	0.00‰	0.00‰	1.27	0.13	247.3	31.5	120.0	32.2		
	B	40‰	39.2‰	24.5‰	1.7‰	0.00‰	0.00‰	1.62	0.13					3.4	41.8/10.9
	I	14.2‰	40.5‰	34.2‰	7‰	0.29‰	0.05‰	1.10	0.16	459.2	43.3	206.6	47.4		
P4	E	34.8‰	46.7‰	23.8‰	0.9‰	0.00‰	0.00‰	1.54	0.11	524.8	52.0	99.7	43.7		
	B	47.6‰	33.6‰	17.2‰	0.4‰	0.00‰	0.00‰	1.90	0.11					3.2	32.3/7.0
	I	10.2‰	46.2‰	38.6‰	10.4‰	0.23‰	0.05‰	0.96	0.13	540.0	70.2	173.0	47.5		
P5	E	20.4‰	43.4‰	30.2‰	2.4‰	0.02‰	0.00‰	1.29	0.11	247.3	30.9	109.3	34.8		
	B	38.3‰	33.8‰	21.3‰	1.2‰	0.01‰	0.00‰	1.60	0.09					3.2	32.9/6.3
	I	9.6‰	34.8‰	42.4‰	17.4‰	0.19‰	0.04‰	0.82	0.14	439.1	54.2	287.7	42.9		
P6	E	17.8‰	39‰	37.2‰	10‰	0.10‰	0.05‰	1.03	0.13	252.3	25.6	148.3	28.1		
	B	34.9‰	34.2‰	27.2‰	3.4‰	0.02‰	0.01‰	1.45	0.11					2.7	32.4/6.2
	I	10.5^{a} ‰	35.3^{a}‰	40.3^{a} ‰	11.7^{a} ‰	0.17^{a} ‰	0.05^{a} ‰		0.15^{a}	397.83^{a}	51.21^{a}	184.4^{a}	47.3^{a}		
Total	E	19.2^{b} ‰	40.1^{b}‰	35.1^{a} ‰	5.1^{b} ‰	0.03^{b} ‰	0.02^{b} ‰		0.13^{b}	353.26^{a}	40.63^{a}	110.8^{b}	39.7^{b}		
	B	35.9^{c} ‰	38.6^{b} ‰	23.8^{b} ‰	1.6^{c} ‰	0.01^{b} ‰	0.00^{b} ‰		0.12^{c}						

821 **Table A3.** Correlation (numbers correspond to r^2) of a) infauna and b) epifauna abundance
822 with sediment and plant parameters in *Zostera* interior, *Zostera* edge and bare sand. .
823 Statistically significant is indicated by *p<0.05, **p<0.01, ***p<0.001 and highlighted in
824 bold.

a) INFAUNA	INTERIOR	EDGE	BARE SAND
SEDIMENT			
Very coarse sand	**0.157***	0.062	**0.268****
Coarse sand	0.117	0.037	0.134
Medium sand	**0.171***	0.071	**0.251****
Fine sand	0.121	0.092	0.102
Organic content	<0.001	0.059	**0.205***
PLANT			
Shoot density	0.062	0.045	
AB	0.002	0.017	
BB	0.005	0.082	
Shoot length	0.046	0.020	

825

b) EPIFAUNA	INTERIOR	EDGE
SEDIMENT		
Very coarse sand	0.002	**0.464****
Coarse sand	0.004	0.150
Medium sand	0.001	**0.573*****
Fine sand	0.008	**0.451****
Organic content	0.022	**0.570*****
PLANT		
Shoot density	**0.230***	0.014
AB	**0.234***	0.072
Shoot length	<0.001	0.053

826
827
828
829
830
831
832
833
834
835
836
837
838

Table A4. Dissimilarities between a) overall *Zostera* interior (I) and bare sand (B). b) patch P4 *Zostera* interior and patch P4 bare sand. and c) patch P1 (least exposed) and patch P4 (most exposed) *Zostera* interior infaunal communities. For each sub-table corresponding average contributions of the 4 most pivotal taxa to habitat dissimilarities are listed. While a) highlights the infaunal taxa generally benefiting from seagrass beds as biogenic habitat, b) reveals the main taxonomic differences between *Zostera* interior and bare sand habitats at the most exposed position. Sub-table c) on the other hand outlines the infaunal taxa associated with *Zostera* that show highest changes in abundance between the least and most exposed patch.

a) Interior and Bare sand total						
Average dissimilarity =46.00	I	B				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Pygospio elegans	2.99	1.22	6.51	1.50	14.16	14.16
Hydrobia spp.	2.87	1.64	5.46	1.31	11.87	26.02
Oligochaeta	2.57	1.81	5.12	1.40	11.14	37.16
Cerastoderma glaucum	1.60	0.59	4.28	1.46	9.30	46.46

b) Interior high stress (P4) and Bare sand high stress (P4)						
Average dissimilarity = 53.49	I (P4)	B (P4)				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corophium volutator	2.82	0.00	8.37	1.76	15.64	15.64
Hydrobia spp.	3.76	1.48	7.85	1.57	14.67	30.31
Oligochaeta	3.17	1.49	7.39	1.96	13.81	44.12
Pygospio elegans	2.62	0.68	5.97	1.99	11.16	55.28

c) Interior low stress (P1) and Interior high stress (P4)						
Average dissimilarity = 38.77	I (P1)	I (P4)				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corophium volutator	0.20	2.82	6.49	1.73	16.73	16.73
Oligochaeta	2.22	3.17	5.19	1.30	13.39	30.11
Potamopygrus antipodarum	1.78	0.28	4.33	1.37	11.16	41.28
Hydrobia spp.	2.82	3.76	2.98	1.54	7.70	48.97

Table A5. ANOVA results for difference in overall community (dis-)similarity between *Zostera* interior (I), *Zostera* edge (E) and bare sand (B).

Variable	F	P	Tukey HSD
Similarity within patches	6.705	0.0083	I > B*, E > B**
Dissimilarity between patches	40.15	<0.0001	B > I***, B > E***

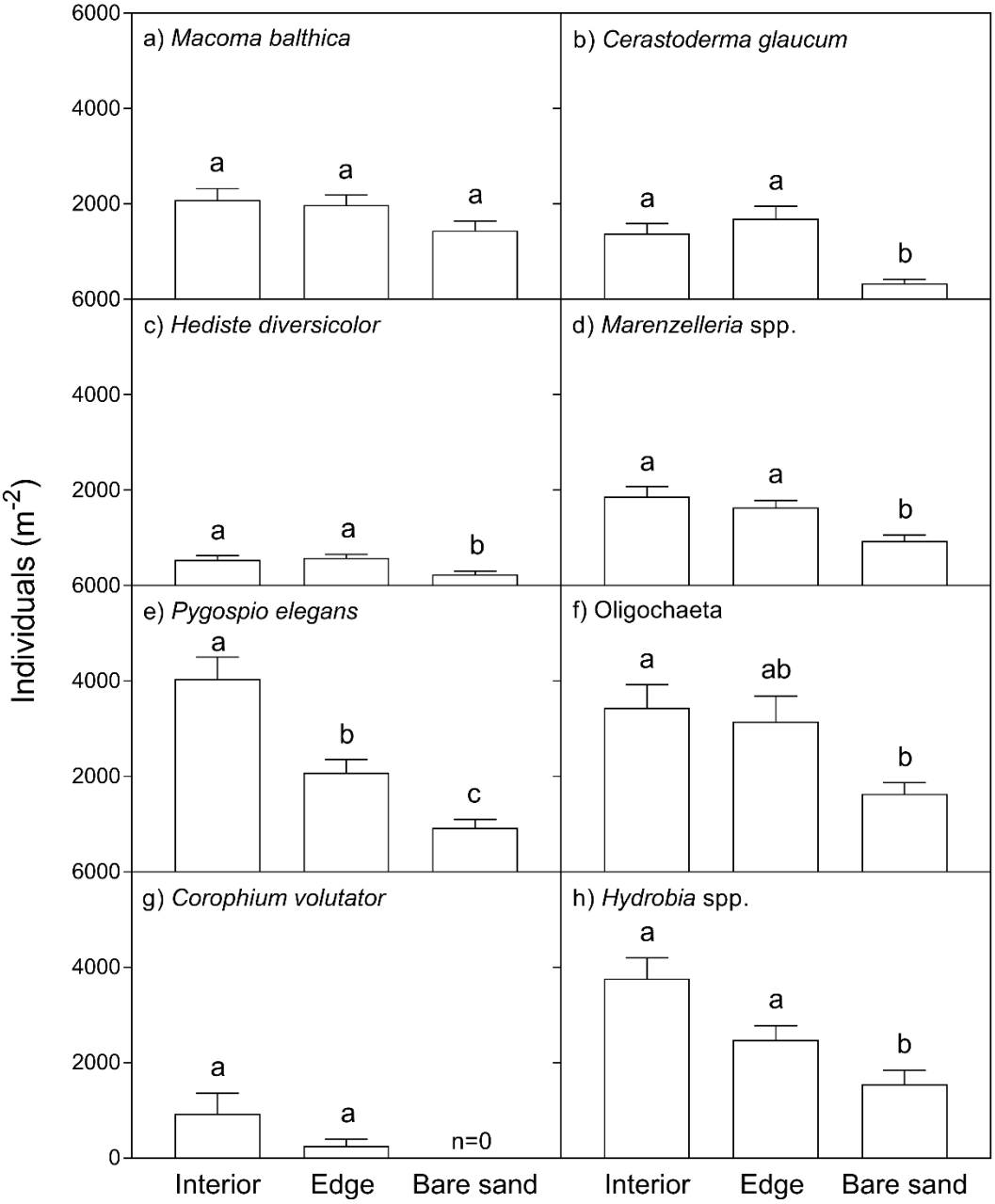
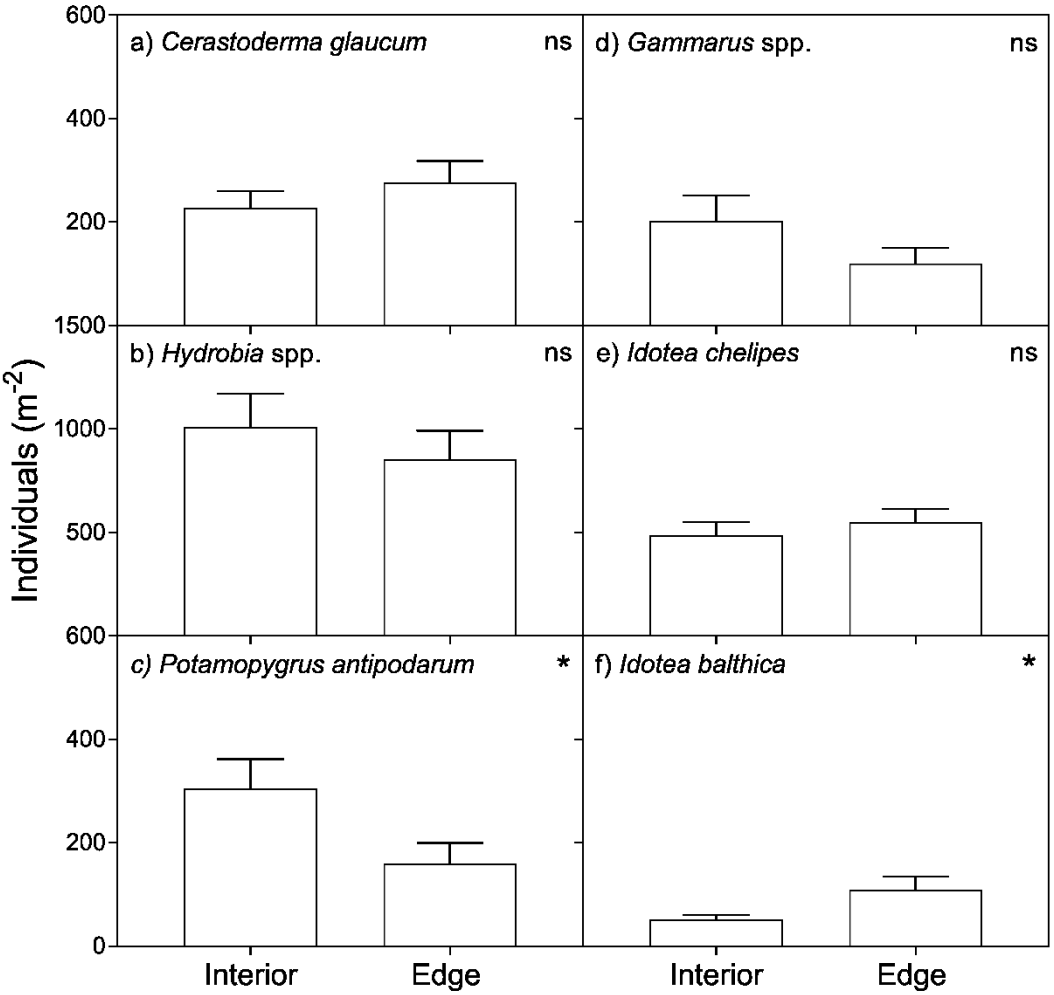


Figure A1. Mean abundance of most abundant infauna species in the *Zostera* interior, *Zostera* edge and bare sand habitats (n=30 for Interior and Edge and n=29 for Bare sand) ± SE. Different letters above bar plots indicate significant differences ($p<0.05$).



861

862 **Figure A2.** Mean abundance of most abundant epifauna species in the *Zostera* interior and
863 *Zostera* edge (n=18 for each habitat) ± SE. Significant differences are indicated with *
864 ($p<0.05$).

865

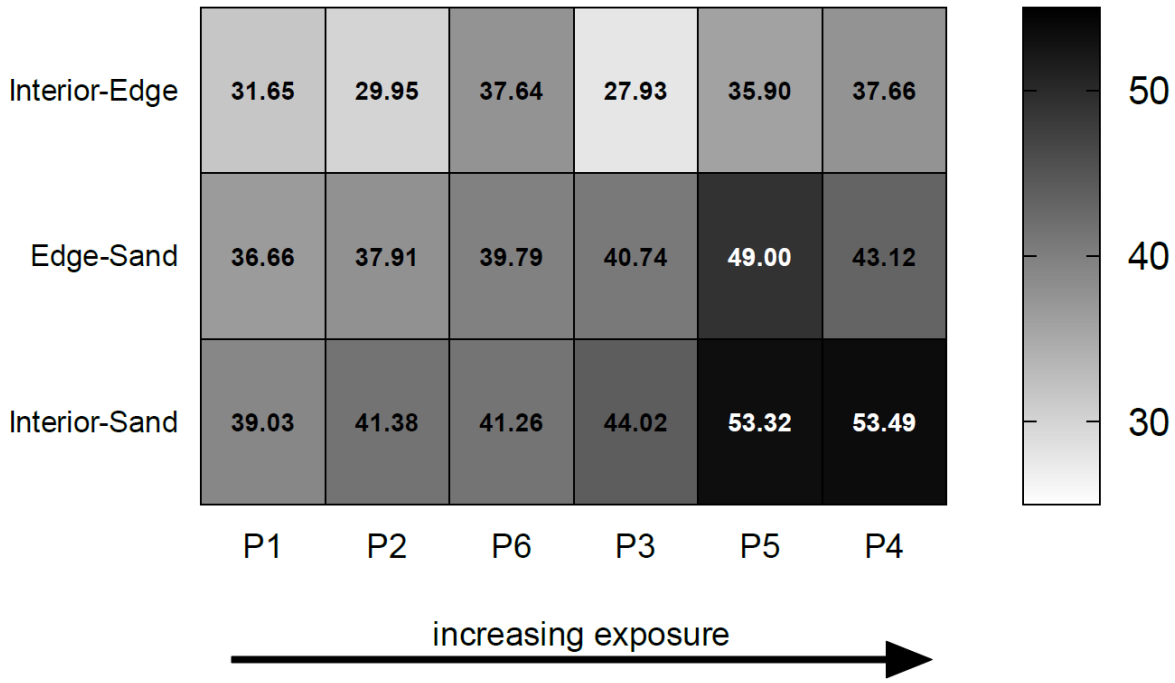


Figure A3. Dissimilarity percentages of the infaunal community between habitats (*Zostera* interior. *Zostera* edge. bare sand) along the 6 *Zostera* patches obtained by SIMPER analysis. The underlying Bray-Curtis measure of dissimilarity is based on square-root transformed abundance data. The patches P1-6 are re-ordered along the exposure gradient (as described by PC1) from least (P1) to most exposed (P4).